## The Locus of Cell Mechanisms

In opposition, Remak (1852) contended that the nucleus itself divided prior to cell division but noted, "Observations on the mechanisms of nuclear division are by no means so extensive as those on the behaviour of the cell membranes" (translated by Harris, 1999, p. 139). Three years later he contended that nuclear division was preceded by division of the nucleolus through a process of constriction and nuclear membrane partitioning analogous to that found in division of the cell body (Remak, 1855).

One of the first microscopists to contend that the division of the nucleus was more complex than a simple division was Wilhelm Hofmeister (1849). He observed in pollen mother and staminal hair cells of *Tradescantia*, a plant used for ground cover, that the nuclear membrane dissolved before the cell divided. If he stained the cell with iodine, however, he could observe discrete lumps (*Klumpen*, presumably chromosomes) that Hofmeister proposed were protein coagulates. He reported that a *granular mucilage* formed around these lumps and divided into two, with a membrane forming around each as the cell divided.

The availability of fixatives, stains, and finally apochromatic lenses enabled research on nuclear processes in cell division to explode in the 1870s and 1880s. Edouard van Beneden (1875) characterized the structures in the nucleus as little rods (*bâtonnets*) and observed that they moved apart in the process of nuclear division. Working with fertilized eggs of the marine mollusk *Geryonia*, Hermann Fol (1873) described the configuration of the spindle and astral rays and proposed an analogy with the lines of force found between opposite magnetic poles, suggesting thereby a dynamical perspective. Focusing on cell division in conifer embryos, Eduard Strasburger, in the first edition of his *Zellbildung und Zelltheilung*, presented drawings portraying a fibrous spindle at several stages of division.

Walther Flemming (1878; 1879) devoted considerable effort to developing new fixatives that would better reveal the details of the process of nuclear division. The product was a mixture of chromic, osmic, and glacial acetic acids that came to be known as Flemming's solution. Because the rods responded to this and other stains, Flemming referred to them as *chromatin*, contrasting them with unstained structures he labeled *achromatin*. (Waldeyer, 1888, gave them their current name, chromosomes.) Working with salamander larval epithelial cells, Flemming observed that the rods split lengthwise and proposed that one half went to each of the two daughter cells. To distinguish this far more complex sequence of events from the simple form of nuclear division described by Remak, Flemming referred to the process as "indirect nuclear division" and introduced the term "*Karyomitose*" for the changes in the chromatin. Flemming reviewed his findings and presented several detailed figures of the